On so-called "Quintocubitalism" in the Wing of Birds; with special reference to the *Columbæ*, and Notes on Anatomy.

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[Read 16th March, 1899.]

(Plates **12** & **13**.)

Since the results of Wray's investigations were published (**1**), the occurrence of two well-marked modes of disposition of the quill-feathers on the upper part of the wing of birds has been well known, and the explanation of the existence of the two conditions has been sought by many zoologists. In one mode of disposition, that known as "quintocubitalism," the quill-feathers which abut on the ulna are arranged in a regular and even series, each feather with its upper and lower covert being of approximately the same size and lying at the same approximate distance from its neighbours on the distal and proximal sides. In the disposition termed "aquintocubital" the first four quills, counting from the distal towards the proximal end of the ulna, are arranged precisely as in the quintocubital wing, but, after the fourth, there is a gap in which there is an upper and lower covert precisely as in the regular arrangement but no quill between them. Thereafter the quills follow in regular series. It appears as if the fifth quill had been lost without any other disturbance of the series, and the condition was called "aquintocubital," *i. e.* without the fifth cubital, on account of this ready interpretation. It appears to me that it would be more convenient to state the facts in another way. Immediately distad of the cubital quills

* [This Memoir is complementary to that by Mr. W. P. Pycraft, which follows (*infra*, pp. 236–254). During the autumn of 1898, Mr. Pycraft intimated his intention of early presenting to the Society a memoir on the so-called Aquintocubitalism in the Bird's wing, and in subsequent conversation with Mr. Mitchell he discovered that the latter had already arrived at the same main conclusion as himself, and that he had lodged a preliminary statement concerning it with the Editor of a scientific journal. When these facts became known to the Officers of the Linnean Society, they approached the two gentlemen with a proposal that their memoirs might be presented at one of the Society's meetings and published together in its Journal, and to this they willingly agreed, Mr. Chalmers Mitchell very generously withdrawing the afore-mentioned press notice.

Except that the authors agree on the main issue, to which they came "independently and unknown to one another," their papers will be found to supplement each other—one author having approached the subject through the study of development, the other through that of adult anatomy.—Ed.]

there is a variable remex, which when normally developed, as in *Nothura*, is in obvious series with the cubital remiges, and which is frequently smaller in size but connected to the cubital series by a special plica of membrane as in most pigeons, but which may be absent; although in the case of the Columbæ, to which this memoir has special reference, I have not noticed a case of absence. I believe the simplest way to state the facts is to adhere strictly to the division of the remiges or wing-quills into primaries and secondaries, to consider the carpal remex as the first secondary, and then to say that, after the fifth secondary, there may be a gap more or less equivalent to the space which would be occupied by a sixth secondary in even series, after which the secondaries continue in normal series; or that the secondaries may all lie in normal series without the occurrence of a gap. For the first condition, that hitherto known as "aquintocubital," I propose the term "*diastataxic*"; for the second condition, that known as "quintocubital," I propose the term "*eutaxic*." These new terms are simply descriptive; they convey no implication as to the way in which the two conditions arose, and they appear to me to be equally applicable, whether we accept the current view that the diastataxic condition has come about by the disappearance of a fifth secondary from an eutaxic series, or if, as I believe, there is no lost feather. If there be no missing feather, it is obvious that the diastataxic condition might have arisen from the eutaxic condition by elongation of the wing in the region of the gap without the addition of a quill to the series; or that the eutaxic condition might have come from a diastataxic condition by the closing-up of the quills without consequent obliteration of the gap. I hope in this memoir to show reasons for the latter view—for, in fact, the view that the diastataxic condition is architaxic.

For some time I have been engaged in a special study of the Columbæ. These, like most of the larger groups of birds, have been described as diastataxic, and, without question, the wing in the majority of them presents a well-marked gap. This is well seen in the wing of a common pigeon, where the gap is as large as in a duck or in an eagle, and is occupied by an apparently normal covert. In *Turtur chinensis* (Pl. 13. fig. 7) there are ten primaries with their major coverts placed (as I find invariably among the Columbidæ) distally to the corresponding quills; then comes a moderately-sized carpal remex bound down by a special fold of the wing-membrane to the next secondary; the carpal covert is, like all the secondary major coverts, proximad of the corresponding quill in insertion. After the carpal remex there follow four secondaries, then a gap which is slightly exaggerated in the drawing, then six other secondaries in even series. The major covert in the gap is bound to the major covert proximal to it by a thin slip of membrane. In *Geotrygon montana* (Pl. **13**. fig. 5) the carpal covert is very small, and under it lies a small remex bound down to the next secondary in normal fashion. Then follow twelve secondaries placed at almost equal distances, so that at first sight the arrangement appears to be eutaxic. Examination of the interspaces, however, shows that there is a small additional covert clearly belonging to the major series but with no corresponding quill. The same condition is very plain in *Œna capensis*; it is only the presence of the covert that makes it possible to regard the wing as diastataxic. The odd covert is plainly crowded, a condition which is still more plain in the specimen than in the diagram, in which for convenience of drawing the relative size of the feathers as compared with the interspaces has been minimized. I have found in a certain number of the Columbæ that the wing is practically the same as in *Geotrygon* and *Œna*, with the most important difference that there appears to be no extra covert, and that, in consequence, the wing must be regarded as eutaxic, and the group Columbidæ added to those among which both eutaxic and diastataxic conditions occur. Nearly two years ago, when I found this eutaxic condition in *Columbula picui*, I showed the specimens to my friend Mr. Beddard, in whose laboratory in the Zoological Gardens I was prosecuting my work, and with my consent he noticed the observation in his recent work on Birds (2. p. 305). With that exception the observation is new to literature, and since then I have found the same condition in a number of other pigeons. In *Geopelia cuneata* (Pl. **12**. fig. 1) and in *G. tranquilla* there are ten primaries, each with a distal major covert; then comes the small carpal covert and remex, the latter with its usual slip binding it to the adjacent secondary; then follow in even series ten fully-developed secondaries, each with normal proximally-placed major coverts, and in the diastataxic interspace there is neither any trace of gap nor an extra covert. In *Leucosarcia picata* (Pl. **13**. fig. 2) the conditions are identical, except that there are eleven fully-developed secondaries. In *Geophaps plumifera* (Pl. **13**. fig. 3) the same condition exists, except that there are twelve fully-developed secondary quills. In *Columbula picui* there are ten primaries and also twelve fully-developed secondaries. In *Starnœnas cyanocephala* (Pl. **13**. fig. 6) there are ten primaries, then an unusually large carpal remex with the normal binding fold and covered by a small carpal covert; then follow twelve fully-developed secondaries without any trace of the diastataxic gap. In *Phlogœnas cruentata* there are nine primaries, then a normal covert and remex, then twelve fully-formed secondaries, with no trace of the gap.

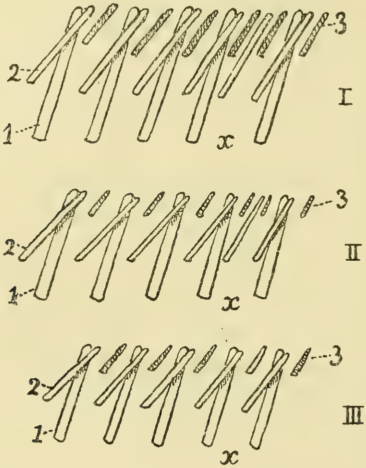
It appears, then, that the Columbæ form an interesting addition to Kingfishers and Swifts, some members of which groups exhibit the one condition, others the other; and it is among such groups that we may hope to find an explanation of the divergence in structure *. The mere statement of the facts as they occur among the Columbæ seems to me at once to suggest an extremely probable explanation. In most pigeons the wing is diastataxic, with a large gap occupied by a "covert." In some pigeons (e. g. *Œna* and *Geotrygon*) there is practically no gap but a covert crowded into the interspace which forms the gap in most pigeons; in *Geopelia cuneata* and *G. tranquilla*, in *Columbula*, *Leucosarcia*, *Starnœnas*, *Geophaps*, and *Phlogœnas* there is no gap, and there is apparently no extra covert.

It is now necessary to consider a third row of feathers, for simplicity not represented in the figures in the Plates, but shown in fig. 1 in the text. Lying apparently in between the quills and coverts, but really belonging to a more dorsal series, there is a small feather marked 3 in the figure; except in the gap marked x there is plenty of room for these third-series feathers. In the gap, even in a diastataxic bird (fig. 1, I), there is a certain crowding of these feathers, which are rather smaller than the others of their series. In a diastataxic bird where there is no actual gap, as in *Œna* or *Geotrygon* (fig. 1, II), the two feathers on either side of the actual covert are exceedingly crowded, and are markedly degenerate, relatively much more so than in the diagram, while the covert itself is smaller in size. In the eutaxic birds (fig. 1, III) there is only one feather in this interspace; as a result the interspace does not differ from the other interspaces. Which of the three crowded feathers has remained I cannot be certain, but I think it probable that it is

* The late Mr. Seebohm made the suggestion that eutaxic species may possibly have arisen from diastataxic ancestors by suppression of the coverts (Classification of Birds, 1895, Suppl. p. 8).

the so-called diastataxic covert in a form so much reduced as to appear to be one of the ordinary third series. My explanation is, then, that pigeons were originally diastataxic with a full gap occupied by one feather of the upper-covert series and two small feathers of the third series. In some pigeons there has been a closing-up of the ranks of quills so that there is no actual gap in the diastataxic space, while into this reduced space there are

Fig. 1.



I. Diagram of secondaries (1), coverts (2), third-series feathers (3), in Columbæ; *x*, diastataxic gap. Complete diastataxic condition.

II. *Geotrygon*: same lettering, showing reduced diastataxic gap (*x*) with three crowded feathers in it.

III. *Leucosarcia*: same lettering. Eutaxic condition. No gap in the inter-space (*x*), and only one feather, which may be one of series 3, or 2.

crowded three feathers, the two smaller markedly reduced and the covert itself not seldom noticeably smaller. Finally, a certain number of pigeons have become absolutely eutaxic by the suppression of the two smaller feathers, leaving the covert in a reduced form, or at least by the suppression of two of the three feathers. The eutaxic condition is a modification of the more primitive diastataxic condition, and intermediate conditions occur.

Systematic Position of the Eutaxic Pigeons.

The nomenclature I have followed is that used in the 'List of Animals' published by the Zoological Society, as I obtained my specimens from the Zoological Society's Gardens. These names are identical with those in the British Museum Catalogue, except in the cases of the bird I name *Phlogœnas cruentata,* which is there called *P. luzonica*, and the bird I name *Geophaps plumifera*, which is there named *Lophophaps plumifera.*

Garrod (3) considered the classification of pigeons from the point of view of anatomy. He does not place *Geophaps*, but of the other eutaxic forms, *Leucosarcia* is placed in his family *Phapidæ*, and the others each in a different division of his family *Treronidæ.* According to the British Museum system, all the eutaxic forms belong to the family *Peristeridæ* but are distributed among four different subfamilies. It is clear that these eutaxic forms cannot be regarded as forming a separate group by themselves. Here and there, almost at random, among the great mass of diastataxic forms occur a few eutaxic forms. If, as I have attempted to show in the earlier part of this paper, the eutaxic condition be a simple derivative of the diastataxic condition, then it is not surprising to find that quite different genera are convergent in this respect. I shall now show that there is considerable reason, based on anatomy, for regarding these eutaxic pigeons as convergent in other respects.

Anatomical Reasons for the supposition that Eutaxic Pigeons are not Primitive.

To avoid constant repetition of the names of the seven pigeons the wing of which displays the eutaxic condition, I shall refer to them according to the following list:—

Geopelia cuneata	A.
Geopelia tranquilla	*a*.
Phlogœnas cruentata } *Phlogœnas ? luzonica* }	B.
Starnœnas cyanocephala	C.
Geophaps plumifera } *? Lophophaps* ,, }	D.
Columbula picui	E.
Leucosarcia picata	F.

When the anatomical differences presented by a large number of closely-related individuals are considered, it is generally possible to come to a conclusion as to what conditions are more primitive and what are secondary. In different groups certain structures are on the wane, others are in process of development, and such general changes appear to characterize whole groups; the complete assemblage of related animals appears to be moving in the same direction; the same structures appear to be in process of advancement or of degeneration, so that the special characters of the whole group tend to become more and more accentuated. In this general progress, individual species or genera may advance specially rapidly or may lag behind; and those which are most or least advanced in the direction of the whole group are by no means necessarily most closely related to one another, although in the structures most affected by the general course of the changes, strong convergent resemblances result. In the case of pigeons for instance, there are anatomical considerations by which one may consider particular individuals or species more or less "pigeony" pigeons (to coin a convenient inelegancy), and the species which are most "pigeony" are not specially related one to the other. For some time I have been engaged on the anatomy of this group with the special view of tracing such progressive advances and degenerations. The work involves dissection of many hundreds of individuals, and it will be long before I am in a position to publish final results. There are many sources of error, some of which can be eliminated only by comparison of the anatomy of many individuals of the same species and the same variety. I have for the present purpose drawn on my notes only for such points as appear to me to be unusually clear; and in this way, although I leave out many features which I have no personal doubt will prove of interest, I gain in immediate certainty and brevity. The general conclusion to which I come is that the eutaxic forms display a number of anatomical features which show them to be well to the front among pigeons generally in the progressive changes for which evidence is to be found among pigeons—that, in fact, they are more "pigeony" than their diastataxic allies. I do not mean that every eutaxic pigeon exhibits every progressive advance or degeneration more notably than every diastataxic form, but that on the whole they do exhibit such changes in an unusual degree.

In the argument which I am attempting to develop there is the apparent flaw that advance in one direction is not necessarily associated with advance in other anatomical structures. It is a familiar condition to find extreme specialization in certain directions associated with extremely primitive conditions in other directions. From this point of view, it might be said that even were the eutaxic condition primitive it would not be surprising to find that birds primitive in that respect were much specialized in other directions. I am not yet prepared to meet this argument fully in its application to pigeons; I can only say that I find that where the lines of progressive change are clear, there appears to me to be a high average of association among the changes. Taking only the changes characteristic in a group, individuals with one of the changes well marked have a high average of the other changes. Groups are, in fact, characterized by a tendency to particular variations in particular structures; these variations are individual and in a state of flux in the more primitive species, but tend to become fixed as specific or generic characters in more advanced types.

Muscular Anatomy.

M. rhomboideus superficialis.—In the majority of *Columbidæ* according to Fürbringer (4), and I am able to corroborate him, the origin of this muscle is fleshy. In A, *a*, B, C, and E it has become tendinous, while in E part of the anterior end of the muscle is a degenerate fibrous sheet. In the vast majority of birds this muscle has passed into what is certainly the secondary condition of being tendinous in origin. The Columbæ are peculiar in that most of them present the more primitive condition, but in five out of the seven eutaxic forms this primitive condition has been lost.

M. supracoracoideus.—The great development of this muscle is one of the special features of the anatomy of the Columbæ. In its highest development, it extends to the extreme tip of the sternum and invades the keel to a considerable extent. A special feature, which will be noticed with the osteology, is the tendency to formation of a strong smooth ridge of insertion which carries the line of the coracoid across the anterior edge of the keel. In all the seven eutaxic pigeons the muscle and its ridges has reached the extreme development found in the group. Associated with this extreme development is a markedly bipinnate arrangement of the muscle-fibres on their central tendon; the extent to which this occurs varies among pigeons, but is strongly marked in all the eutaxial forms.

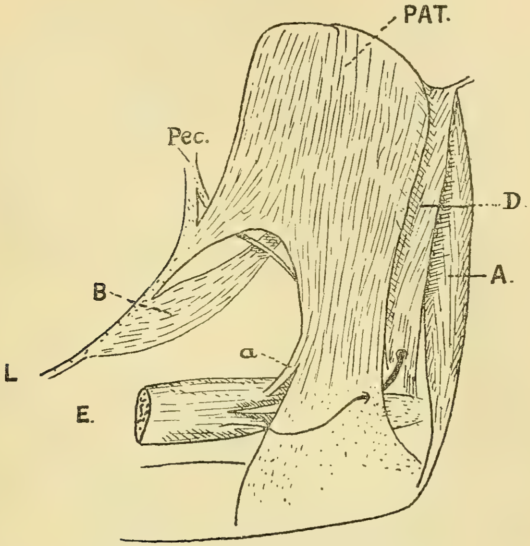
M. coracobrachialis externus.—This muscle from the coracoid to the planum bicipitalis of the humerus is a large muscle in Ratites, but in Carinates is on the wane, entirely disappearing in some of the Passeres. In the Columbæ generally it is very small and partly covered by the biceps tendon, but frequently possesses a fair proportion of muscular fibres. In all the eutaxic pigeons it is extremely small, in some of them being practically reduced to a tendon.

M. latissimus dorsi anterior et posterior.—These muscles are extremely variable among birds, and pigeons show a considerable range of difference. The general tendency among them is for the anterior muscle, originally narrow and strap-like, to extend its origin and to broaden out; the posterior, on the other hand, is becoming reduced. In all the eutaxic pigeons, the anterior muscle has a fairly broad origin ranging from about the third last cervical, or just in front of that, to the first or second dorsal. In this respect these pigeons cannot be said to be markedly in front of the diastataxic forms, but they occupy an advanced place among the progressive forms. On the other hand, they are all markedly advanced in the degeneration of the posterior muscle. In E there is a slight fibrous representative of it, in the others it is completely absent. In diastataxic forms it is frequently present, with distinct origin and insertion; in *Columba* it is variable individually and specifically.

Group of Alar Muscles.—In the angle between the humerus and forearm there are a number of muscular structures to which great attention has been paid by Garrod, Gadow, Fürbringer, Beddard, and others; and those structures have been shown to possess considerable systematic value. In pigeons generally there is great variety in the component parts of this group of structures, and the differences both in their general aspect and in their individual details have great significance. The general tendency undoubtedly is to increase the musculature attached nearer the proximal end of the forearm and to decrease that more distally inserted. The mechanical effect of these changes, which obviously are progressive in the group, is to strengthen the muscular pull, which from its insertion nearer the fulcrum increases the rapidity of the upward movement of the forearm on the humerus. In this general tendency towards change, a more Passerine-like condition is being attained by many pigeons. The eutaxic pigeons show the changes, some of them in an extreme form, all of them notably; and in this respect it is interesting to remember that the Passerines are a eutaxic group.

Biceps patagialis.—This important patagial muscle is in origin a slip from the biceps brachialis which runs to the long tendon of the deltoides patagialis. In fig. 2 B, I show it in a condition which is usually primitive among pigeons, and which I found as an individual abnormality in *Columba livia*. The whole slip

Fig. 2.

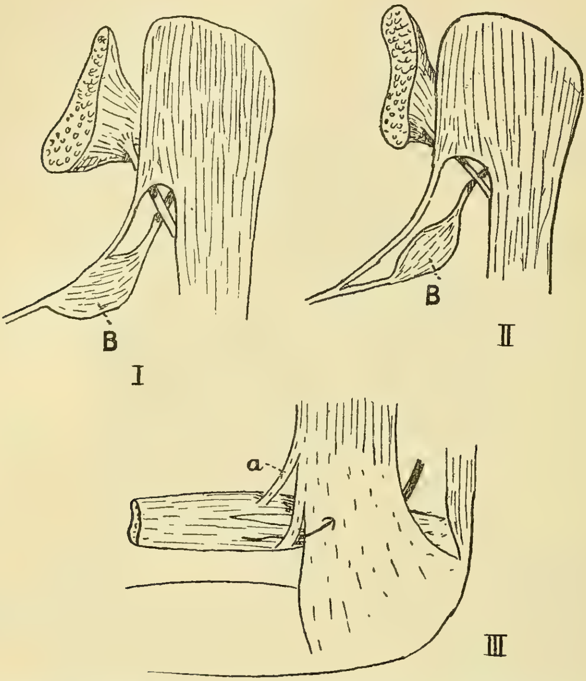


Alar muscles of *Columba livia*.

PAT. Deltoides patagialis. Pec. Pectoralis propatagialis. B. Biceps patagialis slip, an unusually primitive condition not common in *Columba livia*. L. Longus tendon. A. Anconæus scapularis. D. Deltoides major. E. Extensor metacarpi radialis. *a*. Fürbringer's 'alpha' slip.

from its origin to insertion is muscular. In fig. 3 I the normal pigeon-condition is shown. The origin from the biceps is reduced to a rounded tendon or even a thin aponeurosis arising partly from the wing-membrane. In fig. 3 II the most advanced pigeon-development is represented. The muscle is now fully specialized, and has a long tendon at each end with a considerable muscular belly. The insertion is now very low down on the longus tendon, the tendon of the biceps slip running parallel with that for a considerable distance. The muscle is in fact losing its primitive function and becoming really more of an accessory to the radial extensors. It appears to me to be a probable suggestion that this extreme development may be tending really to the final extinction of the muscle, and therefore to a Passerine-like condition. My immediate point, however, is that in the eutaxic pigeons the biceps slip tends to be highly specialized. In D the normal pigeon-condition is present; in A, E, and F, the normal insertion with a considerable origin by

Fig. 3.



I. *Geophaps plumifera.* II. *Geopelia tranquilla.* III. *Phlogœnas cruentata,* showing differentiation of brevis tendon into α, β, and γ slips of Fürbringer.

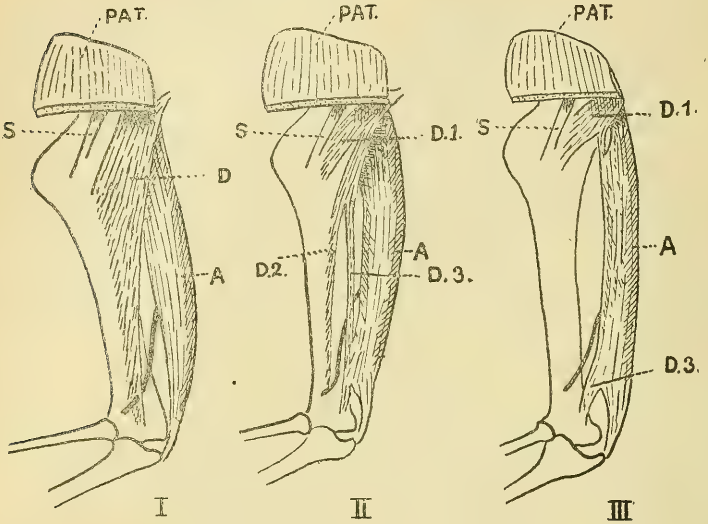
aponeurosis from the wing-membrane; in *a*, B, and C, the extreme development with a long tendon at either end.

Deltoides patagialis.—In fig. 2, Pat., the normal pigeon-condition is shown. The belly of the muscle divides into two peaks, that to the longus being certainly smaller but quite well marked. The distal end of the brevis is divided only into a distal slip running to the extensor, and made known by Fürbringer as 'alpha'; the two slips 'beta' and 'gamma' are not differentiated, but are represented by a single diffuse sheet. In A, *a*, D, E, and F the longus slip is proportionately rather smaller; in B and C it is exceedingly small, almost absent, and the small longus tendon arises almost directly from the general muscle. As for the differentiation of the brevis tendon of insertion into 'alpha,' 'beta,' and 'gamma,' it occurs in A, *a*, B, E, and F, the pectoralis slip forming a considerable portion of 'beta.' In the others the normal condition is attained, not passed.

Pectoralis slip.—In the simple pigeon-condition, as in fig. 2, Pec., the pectoralis muscle gives off two slips partly muscular and continuous at origin, and these run in almost equal proportions to the longus and brevis tendon. The general tendency is for the longus slip to weaken or disappear, and for the brevis slip to become an exceedingly sharply-marked round tendon passing under the deltoides patagialis, and ultimately forming part of the 'alpha' or 'beta' tendon. This ultimate condition recalls that common in Passerines, where there is only a single tendon running to the brevis. The longus part of the patagial is absent in B, C, D, and very short and slight in the others.

Deltoides major.—The series of progressive changes found among pigeons in this muscle are of very great significance and interest. They concern its insertion, size, and subdivision. Typically, the muscle is moderately well developed and is inserted for a varying distance down the humerus. In pigeons there are two grades in its development. In the first grade, as Fürbringer showed, the muscle tends to increase the length of its insertion until ultimately it reaches almost to the distal end of the humerus, where it may be pierced by the large nerve which supplies the forearm. This condition, represented in fig. 4 I, is shown at its maximum in most of the specimens of *Columba livia* which I have dissected, but in some specimens it has not been reached. Among the eutaxic pigeons it occurs in B. In the others, a second series of changes begin. In D the muscle is completely divided into two portions. The upper and smaller portion is inserted to the humerus near the distal end of the supracoracoideus muscle-tendon. In A, *a*, C, E, and F this first part is similarly separated off. The second part in D reaches down the humerus in the usual fashion, but is not actually divided by the radial nerve. In A and F the second part has reached right down the humerus and is pierced by the radial nerve. It is, however, very thin and attenuated, while the deltoides patagialis and anconæus are both unusually large. In E (fig. 4, II) the conditions are similar, but that part of the attenuated long division of the muscle which lies next the anconæus (D. 3) is partly fused with it, although it has a separate insertion. In C and *a* (fig. 4, III) the final stage has been reached. The distal parts of the long division of the muscle have

Fig. 4.



Deltoides muscle.

PAT. Delt. patagialis. S. Tendon of Supracoracoideus. D. Deltoides major. A. Anconæus scapularis.

I. *Columba livia.* II. *Columbula picui.* III. *Geopelia tranquilla.*

apparently quite disappeared, but are represented actually by small slips which leave respectively the distal ends of the deltoides patagialis and the anconæus to be inserted on the distal end of the humerus on either side of the radial nerve. Thus all the eutaxic pigeons show extreme development of this muscle. In six of them it has passed beyond the development into stages of degeneration. It is interesting to notice that in the Passerines there is usually a similar complete division of the deltoid, but I do not know of the existence of stages of degeneration of the long division.

M. metapatagialis or *Expansor secundariorum.*—This curious slip, upon which so much stress was laid by Garrod, is obviously decaying among pigeons. In *Columba livia* it is extremely variable, nearly every condition from full formation to complete absence being present. Traces of it are more common than not among pigeons generally. In the eutaxic forms it is never well developed. Traces of it occur in *a*, B, C, and D; in the others, as in Passeres, it is completely absent.

At this point, I may sum up the evidence from the muscular structure of the wing in the eutaxic pigeons. They all exhibit high stages in the progressive changes to be found among pigeons, and in many of these changes they recall conditions to be found among the Passeres. I do not for a moment wish to suggest that there is any genetic relation between Pigeons and Passeres; but it appears to me that in many points the specialized pigeon-wing shows convergent resemblances to the specialized wing of Passeres. These convergences are peculiarly well marked among the eutaxic forms.

M. ambiens.—This muscle is one of the most interesting and variable structures among birds, and it is only natural to find that the conditions it presents among pigeons are variable and significant. It is impossible to doubt that the pigeons are among that great group of birds characterized by Garrod as Homalogonatæ, from the normal presence in them of an ambiens muscle. Among some Homalogonatous birds (as, for instance, Parrots, Herons, and Storks) the ambiens may be present or absent.

In a former paper (5) I showed that there may be found among Homalogonatous birds, apparently devoid of an ambiens, distinct vestiges of the former existence of that muscle. In another memoir (6) I was able to show that there occurred as individual variations in *Opisthocomus* almost every stage in the degeneration of the muscle, from complete presence to such reduced vestiges as I had described in Parrots and Herons. I do not think it open to doubt that the ambiens muscle is a normal and ancestral constituent of the musculature of pigeons, and that when it is degenerate or rudimentary or absent, such conditions are secondary. In the great majority of pigeons I have dissected it is present in the ordinary form. On the other hand, among the eutaxic pigeons it shows marked traces of reduction. In F alone is it present in the complete normal condition. In *a* and C it is present above the knee in an extremely reduced form; the usual channel through the fasciæ over the knee is absent and the slender tendon disappears. Below the knee, and quite unconnected with the upper part, there is an origin from the head of the fibula representing the usual accessory tendinous head, and from this slips go to the flexors of the toes. In D it is present, but very slender, above the knee, and does not cross the knee-joint, being completely absent below. In B and E it is quite absent above the knee, but below is represented by the fibrous rudiment from the fibula which I made known in Parrots and Herons. In A it is completely absent above and below the knee.

Thus the eutaxic pigeons show a strong tendency to degeneration in this muscle, which is generally present in a fairly well-developed form among diastataxic forms of pigeons. It is interesting to notice that in the eutaxic *Opisthocomus*, which in many respects resembles pigeons, the ambiens is degenerate.

M. peroneus profundus.—This muscle is very variable in birds, and is present in all pigeons; but in the eutaxic forms it is markedly degenerate.

Visceral Anatomy.

I have found no indications of very great importance from the point of view now under consideration. The oil-gland is absent in only one of them (C), but it is small in B and F. It is almost certain that the presence of large cæca is a characteristic of the more primitive forms of the gut in birds (7). In pigeons, generally, the cæca are on the wane, but in the great majority of forms they are definitely present as a pair of nipple-like structures. Among the eutaxic forms they are present in B, but extremely small and showing patches of dark pigment as are to be found frequently on degenerate organs. In C, according to Garrod, they are present; in the only specimen I have seen they were absent, so that it is probable that individual variation occurs. In the other five eutaxic forms they are totally absent. The gall-bladder is absent in all the eutaxic forms, and as it occurs in a comparatively large number of diastataxic forms, its absence may have some significance. In all the eutaxic forms, the gut shows the arrangement of coils and loops which I have described as typical for pigeons (7) in a strongly-marked form. In A, *a*, B, and F the middle loop, so characteristic of pigeons, is particularly long and shows the peculiar spiral twisting in of the parallel distal and proximal limbs in a strongly-marked fashion. So far as the viscera are concerned, it may be said with confidence that the eutaxic pigeons exhibit the typical pigeon-variations in a high degree.

Osteological Characters.

I have not yet proceeded so far with the collection and collation of osteological facts in pigeons as I have done in the case of the muscular anatomy, and I cannot speak with the same conviction as to primitive and ancestral characters, but there are a few definite points upon which the evidence seems to me more clear.

Anastomosis of Dorsal Vertebræ.—In pigeons, as in some other groups of birds, there is a marked tendency to anastomosis of some of the dorsal and posterior cervical vertebræ, with the result of giving a greater rigidity to the vertebral column. This anastomosis affects the vertebral centra, the neural arch, and the articular processes, and is the result of ossification of the ligaments, such as occasionally may be found in old specimens of almost any group. Typically, in pigeons three vertebræ, usually the three anterior dorsals, are anchylosed in this way; and I have not yet found in any diastataxic form a greater number of vertebræ affected. But among the eutaxic forms the fusion has proceeded further. In A, *a*, C, and F it affects four dorsal vertebræ, while in B, D, and E five are united. Similarly, the extent to which the ilia are increased by secondary ossification of the adjoining ligaments and membranes is on the whole more extensive in the eutaxic forms.

Another point of some little importance in pigeons, as in many other groups of birds, is the degeneration of the fibula. I do not think it can be doubted that a fully formed fibula is a primitive character, while degeneration implies secondary modification. This degeneration is usually accompanied by reduction of the deep or second peroneal muscle which springs from a varying area of the distal end of the fibula, and which shows special signs of degeneration among eutaxic pigeons. Beddard and Parsons have shown that the absence of this muscle among Parrots is a feature of systematic importance (8). In Pigeons generally the second peroneal is a strong well-developed muscle, and the ossification of the fibula extends almost to the extreme distal end of the tibia, where it is continued in a strong fibrous band. Among the eutaxic forms, the ossification is never so much as seven-eighths of the length of the tibia, and seldom so much. In A, *a*, B, C, and D it does not reach more than three quarters of the length of the tibia, and the whole bone is very degenerate, the characteristic fusion with the tibia towards the proximal end being specially well marked.

Supracoracoideal crest.—The supracoracoideus muscle (pectoralis secundus) is one which tends to become very highly developed among pigeons. It is well known that its insertion on a special ridge of the humerus is a peculiar feature of pigeon osteology. This ridge is specially well developed among the eutaxic forms, but it would be difficult to say more than that this special development of pigeon anatomy was well marked in them. On the other hand, there is a crest of origin for this muscle to which I cannot find that attention has been directed. In its fullest development it is a T-shaped crest, the stem of the T carrying out the line of the coracoid across the carina of the sternum at right angles to the long axis of that bony protuberance, and the cross-piece of the T lying parallel to the anterior edge of the carina, the lower limb running along the line on the carina which separates the insertion of the two pectoral muscles. This crest is extremely well developed in C, the ventral limb of the cross-piece extending nearly halfway down the carina (fig. 5). In all the eutaxic forms it is

Fig. 5.

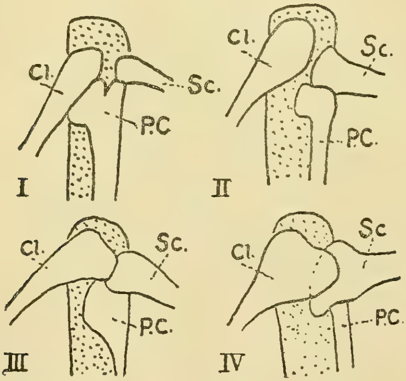
Starnœnas cyanocephala.—Carina of sternum, showing supracoracoideus crest.

very well formed, while the extent of its development among diastataxic forms varies. It is just visible in *Goura* and *Calœnas*; it is well marked, so far as the stem of the T is concerned, in *Columba* and *Turtur*, and in pigeons generally it is noticeable, as in most Passeres. But in the eutaxic forms the stem is always very strong and the lower limb of the cross-piece well marked.

Coraco-sternal articulation.—A primitive feature, familiar in reptiles, is that the coracoids should overlap at their junction with the sternum. This is well marked in some birds, and occurs occasionally among species of *Columba* and in individuals of *C. livia*. In birds generally the coracoids tend to be more and more separated at their sternal articulation. In most pigeons they either actually meet or are very close together indeed. Among the eutaxic forms they just meet in C and E; in the others they either do not touch at all or are well separated.

Angle of Scapula and Coracoid.—This angle varies with the development of certain wing-muscles, and on the whole varies inversely as the power of flight. While it is impossible to lay much stress upon it from the ordinary systematic point of view, it may at least be said that there is a close connection between wide angle and degenerate wings. The angle among pigeons varies considerably; among the eutaxic forms it is never more than 50 angular degrees, and generally is considerably less.

Fig. 6.



I. *Columba*. II. *Phlogœnas*. III. *Leucosarcia*. IV. *Corvus*.—Articulation at shoulder-girdle. The coracoid is dotted. *Cl.* Clavicle. *P.C.* Procoracoid. *Sc.* Scapula.

Procoracoid Process.—Fürbringer has investigated the procoracoid process and the relations of the scapula, coracoid, and clavicle with the greatest care, and has drawn a number of important conclusions from their conditions. It may be said generally that a large procoracoid articulating with the clavicle and a separation of clavicle and scapula are comparatively simple;

while in more specialized forms the procoracoid process becomes smaller, loses its connection with the clavicle, the latter developing an epicleideal plane which meets and may overlap the end of the scapula. In fig. 6 I, a comparatively primitive condition, as seen in *Columba*, and with minor details in most diastataxic pigeons, is represented. The procoracoid is large and articulates prominently with the clavicle, while the latter is not expanded at its end and is well separated from the scapula. In fig. 6 IV, the more advanced condition, as seen in a typical Passerine, is represented. The procoracoid is much reduced, and does not meet the clavicle. The clavicle is expanded at its end, and meets and overlaps the scapula. Among the eutaxic forms, the procoracoid is generally small and never meets the clavicle by a broad articulation, but is either free from it, as in B (fig. 6, II), *a*, C, and E; or just meets it above, as in A, D, and F (fig. 6, III), the junction being in a different place and due rather to the growth of the epicleideal plane than to size of the procoracoid. The clavicle among the eutaxic forms is either quite close to the scapula, on account of growth of the epicleideal plane, as in B (fig. 6, II), or actually meets it, as in the other eutaxic forms (fig. 6, III), while in all the diastataxic forms I have seen it remains separate.

Summary of Anatomical Argument.

When the anatomical differences between eutaxic forms and their diastataxic allies are compared, it appears that the eutaxic forms are on the average distinctly more specialized. If there is any general progress along special lines among pigeons, the eutaxic forms are well advanced. Their anatomical features appear to show that, if eutaxy be a derivative of diastataxy, it is at least a striking coincidence that in other respects eutaxic pigeons are more specialized than diastataxic forms. For my own part I am personally so much impressed by the evidence for the gradual modification of a whole group in the same direction, that I cannot avoid regarding the eutaxy of these pigeons as being simply a part of their general specialization.

Size and Eutaxy.—The eutaxic pigeons, like eutaxic birds generally, are small compared with their allies. A, *a*, D, and E are very small pigeons, B and C are moderately small, and F is the only fair-sized bird. They are certainly smaller than the sand-grouse, which would appear to be the nearest diastataxic allies of pigeons. But, unless one knew the size of the ancestral pigeon, it would be impossible to draw any strong argument from size; in a general way, it may be said that a large number of very primitive birds are large, while many of the most extremely specialized forms are minute, as among the Passeres.

Theory of the Origin of the Diastataxic Condition.

As my general argument involves the supposition that eutaxy is a derivative of diastataxy, it may be worth while to advance a speculation as to the reason why there should have occurred a gap in the wing of birds, and why that gap should be in a fixed position.

The first point upon which I wish to insist is that the quills are not different in kind but only in degree of development, as compared with other feathers. From a uniform covering certain individual feathers have become enlarged to serve the purpose of flight, instead of the more primitive purpose of protection. Precisely in the same way in the case of Elasmobranch fishes, from the general protective covering of toothed scales all over the body, certain individual scales or rows of scales become specially enlarged, and form series of exaggerated teeth, either at special points, as in the case of the dorsal spines of the spiny dogfish, or in rows along the dorsal surface of the tail, as in some skates, or in one or more rows along the edges of the jaws where the external skin folds in to form the stomatodeal lining of the mouth, when such rows are developed. It may fairly be taken for granted that birds had feathers or feather-like scales before they had quills, as quills are simply exaggerated feathers, and that the quills are simply rows of extremely developed feathers.

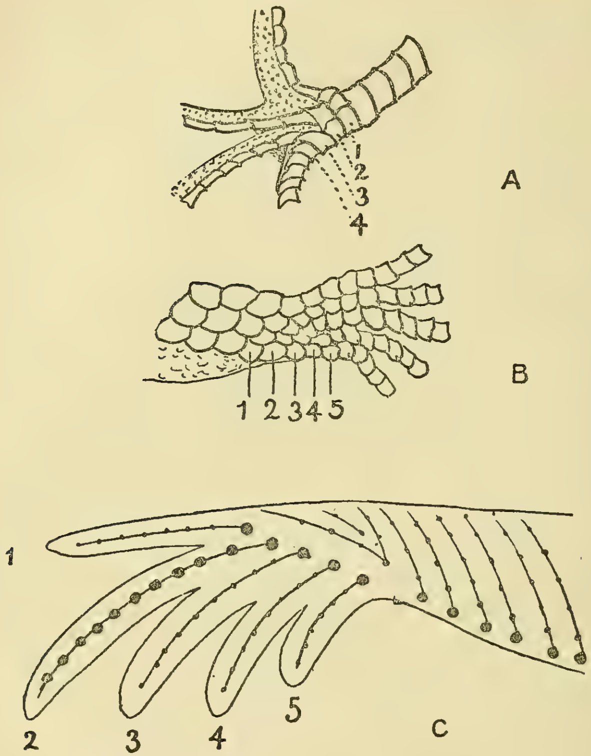
When rows of large structures follow body contours, as in the case of true teeth, caudal spines, or quills, the series appear to possess a longitudinal coherence and integrity which may be fallacious. If pins be placed vertically on diagonal lines crossing the surface of one of the irregular stuffed cushions familiar on old fashioned toilet-tables, the pins which happen to lie along the contour edge appear to have a special symmetry with regard to these contours, and could we imagine these pins to increase in length because of their position, it would be difficult to avoid supposing that the long contour pins were planted specially in a contour row. In the feathering of a wing two series of rows are evident, the intersections of the rows forming a diamond pattern, most conspicuous on the surface of a plucked wing. One series is horizontal, or at least more or less parallel to the contour of the ulnar edge. Of these horizontal series, the rows of quills and of major and second and third coverts are most obvious, partly because of the large size of the individual feathers, but these horizontal rows are much more difficult to trace outside above the larger feathered rows. The other series run rather diagonally to the ulnar edge and are starting upwards and with a forward slope from the quills. They are very beautifully seen in some of Mr. Pycraft's figures (9. plate xxiv.), but are obvious enough in most wings. These diagonal rows run round the surface of the wing posteriorly almost at right angles to its long axis, but anteriorly with an increasingly forward inclination, to which I shall presently refer. They resemble the general disposition of colour-markings or scales on a cylindrical surface which usually occur as hoops running round it; and it appears to me that the apparently longitudinal rows are composed of members of the transverse rows at different levels, being in fact simply the enlarged individuals of the transverse rows which come to lie on the ulnar edge.

In actual development in the wing of the chick, it is true that the two great horizontal rows which are to form the quills and the major coverts appear first as longitudinal rows. It is only when these become obvious, and when one or two other longitudinal rows appear from before backwards, that the diagonal rows begin to be marked. Later on these latter acquire increasing coherence until the adult stage is reached. I am not, however, prepared to attach great importance to this early ontogenetic appearance of the longitudinal rows as such. In the first place, considering what we know of the extraordinary accelerations and retardations that occur during larval development, it would appear to be pushing the recapitulation theory to a ridiculous point, to attempt to found a theory of the ancestral nature of the rows from the order of their ontogenetic appearance. Secondly, there is a very obvious reason for the early appearance of the quill-rows. These and the coverts are much larger than the other feathers; they take longer to grow and must begin first; they are more important to the future bird, and early provision must be made for them.

I suggest that the quills, although appearing to be a horizontal row, are really different members of diagonal transverse series.

There now remains to suggest an explanation of the origin of the gap. In a general way, morphologists have been inclined to regard simple series, as in the case of metameric repetitions, as more primitive than discrete and incoherent series; but in a number of cases, as for instance in the nephridia of earthworms, it would appear that the diffuse condition is simpler and more primitive than the orderly repetition found in the common earthworm. I think we have learned to be on our guard against taking for granted that an apparently simpler condition is in reality more ancestral, and that we should approach the problem of the diastataxic gap without any prejudice in favour of its being secondary. Whether it be secondary or primitive, we have to account not only for its existence but for its appearance in a definite place after five quills. If the primitive condition were eutaxic and the gap produced in a whole series of different birds by secondary lengthening of the wing, we should have to explain why this lengthening always occurred after five quills. If we think of the gap as being primitive, there is no difficulty whatever in supposing that convergent closing should have occurred independently in any number of groups, or even of species and genera; and I think it is not difficult to form some idea as to how a gap in that position might have come into existence in an ancestral wing. Consider an ancestral pentadactyle wing provided with scales or scale-like feathers. The most common arrangement of these, as may be seen by looking at the scales on any lizard or crocodile or on the feet of birds, is that longitudinal rows should run along the digits and diagonal transverse rows should surround the arm. Now these two series have to meet somewhere, and when different series of scales or markings meet, there must be a transition of some kind from one to the other. Sometimes one set of series gives way to the other; sometimes there is intercalated between the two a wedge-shaped set of rows, as Professor D'Arcy Thompson pointed out to me in the case of the markings on the zebra. In the foot of a bird (fig. 7, A) the transverse rows are represented by large single scutes in many cases, while a line of enlarged scutes may run down each digit. Where the digit-scutes come in contact with the other series, they may run down parallel with them and appear on the distal edge of the tarsus. In the arm of a lizard (fig. 7, B) the interference is more strikingly apparent, there

Fig. 7.



A. Foot of a Passerine bird. B. Hand of a Lizard. C. Diagram of scales or feathers on a hypothetical ancestral bird's wing. The quills of modern birds are represented by darker spots.

being along the distal edge five scales which are in series with the digital rows, and there is an abrupt transition from these transverse rows to the modified digital rows. In fig. 7, C represents diagrammatically a simple mode of feather-distribution on a pentadactyle wing which would result in a gap. Rows run along the digits, and where these meet the transverse rows a wedge-shaped piece is intercalated, forming the transition. I have put larger dots to represent the actual quill-series of modern birds. The primaries are the enlarged series of the index digit; the carpal remex belongs to the pollex series; the next four secondaries belong to the digital series of the four digits; then comes a diastataxic gap due to the alteration of curvature (as in the transition from the neck to the body series in a Burchell's zebra) being bridged over by a wedge; then follow the other secondaries, which are members at different levels of the succeeding diagonal rows. Naturally this supposition is entirely theoretical, but it is enough to show that the occurrence of a gap after five quills is a phenomenon which might have arisen in a very simple fashion.

So far as the underlying bones are concerned, the gap in my diagram occurs much more distally than in the adult ordinary bird. I do not think, however, that this presents the slightest difficulty. We know that ontogenetically and phylogenetically the wing of birds elongates. Actually in development the feather-papillæ shift along the wing. Superficial skin-areas generally are exceedingly primitive in their character, but may shift almost indefinitely in their topographical relation to underlying structures. In the human body, these changes of skin-area in topographical position have been worked out in relation to the phenomena of referred pain.

Eutaxy and Diastataxy in Aves generally.

I am not at present prepared to extend the argument from the Columbæ to birds in general at length. But I may point out that there is a general parallel to be found between the relations of eutaxy among Columbine forms and the relations of eutaxy among birds generally. In Columbine forms the majority are diastataxic, and the few eutaxic forms are isolated among their diastataxic congeners. Among the great groups of birds most are diastataxic. We may leave out of consideration the Struthious birds and the Spheniscidæ, as in these the wing is so greatly modified as to make any comparisons misleading, especially as we cannot be certain whether the modifications are from a high, or from a very low type of wing. As for the other eutaxic forms, the great majority of anatomists would agree that the Passeres were extremely specialized birds, and therefore forms in which, if diastataxy be primitive, one would not expect to find it. Similarly the Pici, the Cuculidæ, and *Opisthocomus* are birds in which one would not readily look for primitive features. *Opisthocomus* is an exceedingly peculiar and specialized form. Among the Ralline birds generally, the three eutaxic forms *Psophia*, *Dicholophus*, and *Rhinochetus* present many striking peculiarities which are not generally regarded as primitive, and anatomists generally have regarded them as modified forms of the diastataxic Gruidæ. There remains the great group of Gallinaceous birds, which in many respects, such as the alimentary canal and the completeness of the muscles, present primitive features and are yet eutaxic. On the other hand, they are specialized in the sternum and in the vertebral column. The Anseriformes, which are diastataxic, are quite as primitive in their muscular structure and less specialized in the sternum and vertebral column, while among them are to be found the Palamedeidæ, certainly archaic forms, and sometimes regarded as forming a link between the typical Anseriformes and the Galli. These are diastataxic, as primitive as the Galli in muscular anatomy, more primitive osteologically, and with alimentary canals displaying what appears to be an exceedingly primitive disposition. So far as a general survey goes, there is nothing against and a good deal in favour of supposing that diastataxy is architaxic in Aves generally.

The Alcedinidæ and the Cypselidæ are groups in which, as in the Columbæ, some members are eutaxic, while the others are diastataxic. I have not had an opportunity of dissecting a sufficient number of these forms to obtain an idea as to which condition of the wing is associated with greater specialization.

Summary.

The Columbæ, which have been regarded hitherto as a diastataxic group, have several members with the eutaxic condition. Comparison of the feathering in these forms makes it probable, or at least plausible, that the eutaxic condition has been attained by closing up of the gap, with first crowding, and then disappearance, of two of the three feathers occupying the primitive gap. Intermediate stages between true wide-gapped diastataxic forms and true eutaxic forms occur. Comparison of the anatomy of the eutaxic forms with that of the diastataxic forms shows that the former are on the whole more advanced in the general progressive modification of the whole group. It is easy to show that in a hypothetical pentadactyle wing a gap in specialized rows

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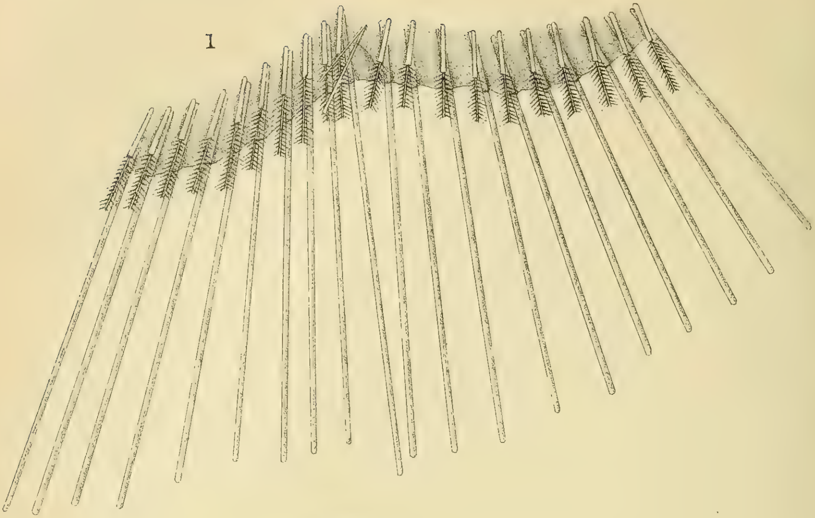

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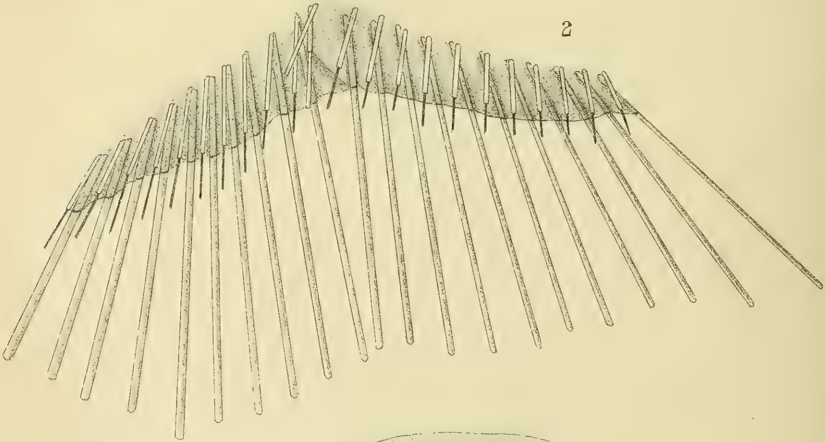

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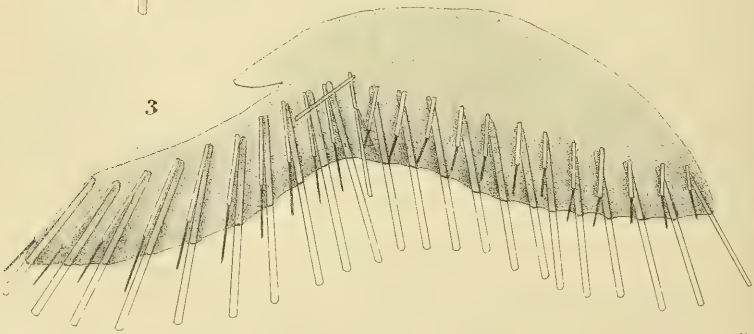

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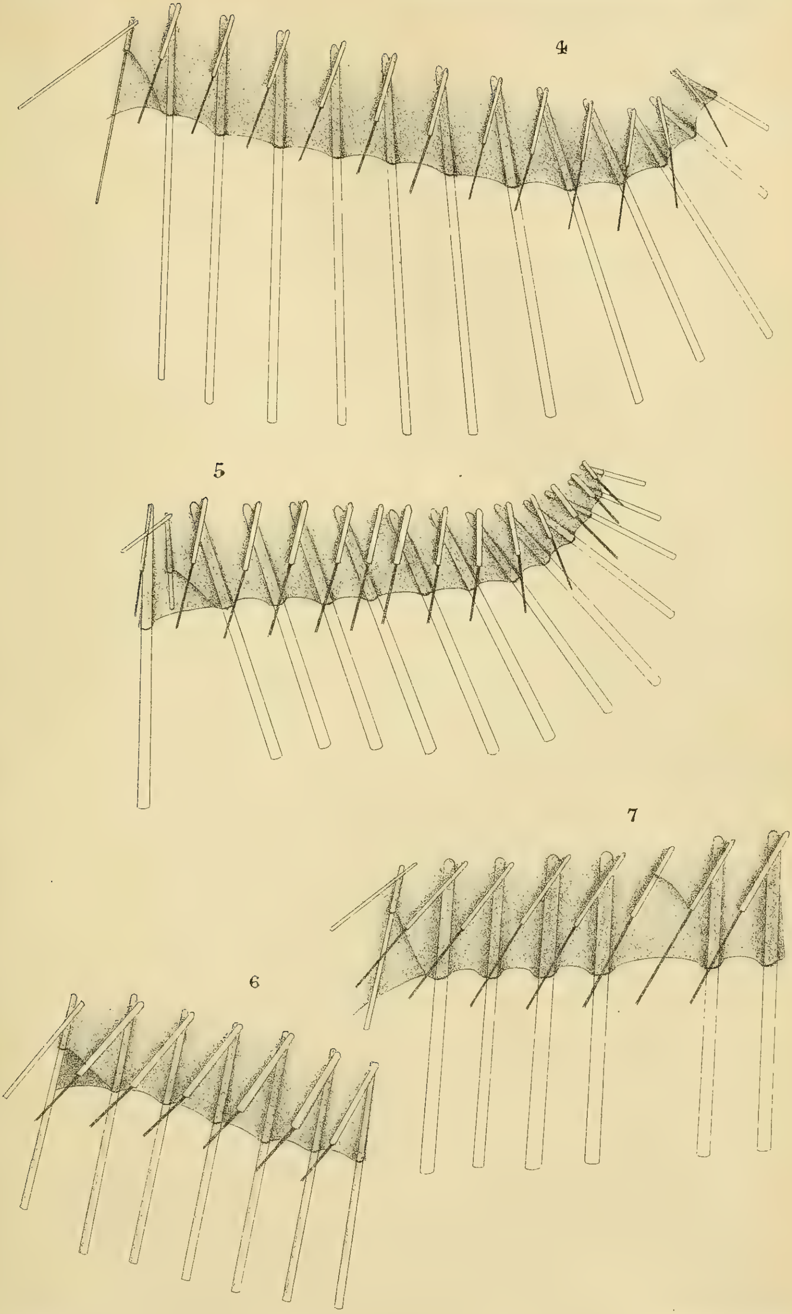

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QUINTOCUBITALISM IN THE WING OF BIRDS.

of incipient quills might arise in the position required for the diastataxic gap. Among Aves there is a general correspondence with the conditions among Columbæ. The diastataxic condition of the wing is primitive among birds; it is the architaxic condition. By closing up of the ranks any architaxic wing may become eutaxic, and this change has been made by some whole groups and by individuals of other groups.

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EXPLANATION OF THE PLATES.

Plate 12.

Fig. 1. *Geopelia cuneata*, left wing: showing primaries and coverts, carpal remex and covert, and even series of secondaries and coverts; no gap. Eutaxic condition.

Fig. 2. *Leucosarcia picata*, left wing: showing primaries and coverts, carpal remex and covert, and even secondary series without gap. Eutaxic condition.

Fig. 3. *Geophaps plumifera*, left wing: showing the primaries and coverts, the carpal remex and covert, the secondaries and coverts without a gap. Eutaxic condition.

PLATE 13.

Fig. 4. *Columbula picui*, left wing; carpal covert and remex; series of coverts and secondaries: showing the eutaxic condition.

Fig. 5. *Geotrygon montana*, left wing; 1st primary; carpal remex and covert; series of secondaries and coverts: showing reduced diastataxic condition.

Fig. 6. *Starnœnas cyanocephala*, left wing; carpal remex and covert; six secondaries and coverts in even series. Eutaxic arrangement.

Fig. 7. *Turtur chinensis*, left wing; carpal covert and remex; four secondaries and coverts; diastataxic gap with covert; two secondaries with coverts.

Some Facts concerning the so-called "Aquintocubitalism" in the Bird's Wing. By W. P. PYCRAFT, A.L.S.*

[Read 16th March, 1899.]

(PLATES 14–16.)

CONTENTS.

Introductory Remarks.

THE feathers in the typical bird's wing, *e. g.*, the Common Fowl, are divisible into two groups—tectrices or coverts, and remiges or flight-feathers, commonly known as "quills."

The remiges form a single row of feathers running along the post-axial border of the wing from the tip of the index-digit inwards to the elbow-joint. Those of the hand constitute the primaries, those of the forearm the secondaries. With the primaries we have little or nothing to do in this connection; suffice it to say that they never, in the Carinatæ, exceed 12 in

* *Cf.* Editorial footnote on p. 21